

The geometry of the Fisher selection dynamics

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Abstract

We study the Fisher model describing natural selection in a population with a diploid structure of a genome by differential-geometric methods. For the selection dynamics we introduce an affine connection which is shown to be the projectively Euclidean and the equiaffine one. The selection dynamics is reformulated similar to the motion of an effective particle moving along the geodesic lines in an 'effective external field' of a tensor type. An exact solution is found to the Fisher equations for the special case of fitness matrix associated to the effect of chromosomal imprinting of mammals. Biological sense of the differential-geometric constructions is discussed. The affine curvature is considered as a direct consequence of an allele coupling in the system. This curving of the selection dynamics geometry is related to an inhomogeneity of the time flow in the course of the selection.

Key words: population dynamics, natural selection
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1 Introduction

The selection dynamics in biological populations was usually investigated by the methods of the dynamic system theory. Apart from simple cases of explicit integrability, the basic problem in such an approach is to find attractors of various types and to study the stability problem [2]. A survey of basic results of the several past decades can be found in monographs [3, 5, 4].

In common practice of selection dynamics, the geometric methods do not attract too much attention, although the importance is stressed sometimes [5, 6].

On the other hand, these methods have demonstrated their efficiency in theoretical and mathematical physics. In modern theoretical physics we observe a trend to formulate dynamical principles (having structural resemblance to the respective biological relations) in terms of differential geometry and Lie algebra. Geometric and algebraic methods provide both suitable mathematical constructions bringing a system to integrability and they facilitate the study of global characteristics of the system. From this standpoint the geometric framework may have considerable interest for the mathematical models of biological systems.

Population models of biological societies display a natural hierarchy regarding to the degree and the character of coupling between system components. In the most general form, the population dynamics should be considered in the context of the ecological system dynamics. The population enters the system as a single element connected with the rest ones by trophic, compete and other links. The system state is characterized by its number, by genetic structure, by age and sex distribution and some other quantities. A complete description of the selection dynamics (the change of the population genetic structure) implies to consider a multi-locus system with all the genes involved in the selection process. To simplify the problem we may consider a single-locus model. A classical example of such a case is the well known Fisher model describing a coupling of alleles of the given locus in the course of the selection. The Darwin system model suggested by Eigen [7] is an utmost case of this simplification. It realizes the basic idea of the natural selection: a differential survive of convariantly self-reduplicating units (according to Timofeev-Resovskii nomenclature [8]), is realized in this model.

In Ref. [9] we develop Hamiltonian form and thereby symplectic geometric description for the selection dynamics in the populations with haploid structure of a genome (when any gene is represented in a single instance (single allele)).

In the geometric framework the evolution of the Darwin system with a stable organization is represented as a motion with a constant velocity in an Euclidean plane space of information variables. This is a result of absence of a coupling between separate genotypes (quasispecies, by Eigen) in the course of the selection.

In the given work the differential-geometrical methods are applied to the Fisher model which is one of the upper level in the above hierarchy with respect to the Eigen model. The Fisher model describes the natural selection in populations with diploid structure of a genome. In this model, the necessary condition for the reproduction (and therefore the selection) of the individuals in the population, is a pairwise coupling of separate haploid genotypes (gametes) by the zygote formation, i.e. the cells or the organisms with the diploid (double) gene setting. The gamete coupling in the population is considered by the Fisher model in terms of pairwise coupling of different alleles of the single gene (single-locus model) or many genes (multi-locus model) being inherited by the individual from its parents.

The basic aim of the paper is to clarify the question how the allele coupling creates the geometry of the space associated with the selection dynamics. We introduce an affine connection related to the first derivative of the Fisher equa-

tions in the population variables space. The affine connection is turn out to be projectively Euclidean one and simultaneously it is an equiaffine connection. The above derivative is presented in the form of equations of motion of an effective particle moving along the geodesic lines in an 'effective external field' of a tensor type. The Fisher equations are integrated for the fitness matrix of a special form associated with the phenomenon of chromosomal imprinting and differential methylation of DNA in the course of the gamete maturation of mammals [10]. In this case the Fisher dynamics is reduced to the dynamics of the Darwin system by a suitable replace of time variable. An approximate solution is constructed in the weak 'external field'. The equiaffinity is shown to result in the conservation of a volume in the population space with respect to the geodesic flows. The volume is defined using a certain density of the affine space.

Mention that the curving of the Euclidean flat space of informational variables is the effect of the allele coupling in the system. This curving could be also interpreted as an effect of the inhomogeneity of the time flow in the in the course of the selection.

2 The Fisher model

Consider a population where the success of reproductivity (and therefore the selection dynamics) is determined by a single gene (locus) having N alleles. Denote by p_α a portion of α -allele in the population, $\alpha, \beta, \dots = 1, \dots, N$. Evidently

$$\sum_{\alpha=1}^N p_\alpha = 1. \quad (1)$$

Choose the quantities p_α as population variables. Then the Fisher system is written as [1]:

$$\dot{p}_\alpha = p_\alpha \left(\sum_{\beta=1}^N \omega_{\alpha\beta} p_\beta - \sum_{\mu, \nu=1}^N \omega_{\mu\nu} p_\mu p_\nu \right). \quad (2)$$

Here $\dot{p}_\alpha = dp_\alpha(t)/dt$, t is the time. The quantity

$$\sum_{\beta=1}^N \omega_{\alpha\beta} p_\beta$$

is the specific rate of reproduction of α -th allele, and

$$\sum_{\mu, \nu=1}^N \omega_{\mu\nu} p_\mu p_\nu$$

is an average specific rate of the population growth as a whole. The matrix $\omega_{\alpha\beta}$ ($= \text{const}$) in the population biology is identified to the fitness matrix associated

with separate alleles. Let us take the N -th allele as a gauge one and introduce the variables

$$z^i = \ln \frac{p_i}{p_N}. \quad (3)$$

Here and below $i, j, k, \dots = 1, \dots, N-1$. The meaning of the variables z^i is that they reflect an information quantity per a degree of freedom in the population in the frame of Shannon formalism [11] (we mean the information about the genetic structure of the population).

Theorem 1 *In the variables (3) the Fisher system (2) is reduced to the form:*

$$\dot{z}^i = \alpha_i + \frac{\sum_k \beta_{ik} \exp(z^k)}{1 + \Omega}. \quad (4)$$

Here,

$$\begin{aligned} \alpha_i &= \omega_{iN} - \omega_{NN}, & \beta_{ik} &= \omega_{ik} - \omega_{Nk} - \omega_{iN} + \omega_{NN}, \\ \Omega &= \sum_k \exp(z^k). \end{aligned} \quad (5)$$

Proof. Introducing the auxiliary variables $y_\alpha = \ln p_\alpha$, we have from (1): $\sum_\alpha \exp(y_\alpha) = 1$. Then $\exp(y_N) = 1 - \sum_k \exp(y_k)$. It is easy to verify that

$$\begin{aligned} \exp(z^i) &= \frac{\exp(y_i)}{1 - \sum_k \exp(y_k)}, & \exp(y_i) &= \frac{\exp(z^i)}{1 + \Omega}, \\ \sum_k \exp(y_k) &= \frac{\Omega}{1 + \Omega}, & \exp(y_N) &= \frac{1}{1 + \Omega}. \end{aligned} \quad (6)$$

Eqs. (2) in the variables y_α take the form:

$$\dot{y}_\alpha = \sum_\beta \omega_{\alpha\beta} \exp(y_\beta) + \sum_{\mu,\nu} \omega_{\mu\nu} \exp(y_\mu + y_\nu). \quad (7)$$

Writing Eqs. (7) for $\alpha = i$ and for $\alpha = N$ and subtracting one from another, we obtain (4) using (6).

3 Projectively Euclidean space

Let us differentiate the system (4) with respect to t and write down the result as follows:

$$\begin{aligned} \ddot{z}^i &= -\frac{1}{2(1 + \Omega)} \sum_{k,l} [\delta_{ik} \exp(z^l) + \delta_{il} \exp(z^k)] \dot{z}^k \dot{z}^l + \\ &\quad \frac{1}{1 + \Omega} \sum_k (\alpha_i + \beta_{ik}) \exp(z^k) \dot{z}^k. \end{aligned} \quad (8)$$

Introduce the affine connection space $\mathcal{A}_{N-1}(\Gamma_{kl}^i)$. In the coordinates z^i the connection is:

$$\Gamma_{kl}^i = \frac{1}{2(1 + \Omega)} [\delta_{ik} \exp(z^l) + \delta_{il} \exp(z^k)]. \quad (9)$$

Eq. (8) has the form of equations of motion for an effective particle moving along the geodesic lines in the affine connection space $\mathcal{A}_{N-1}(\Gamma_{kl}^i)$ with the 'external field' defined by the tensor field A_k^i :

$$\ddot{z}^i + \sum_{kl} \Gamma_{kl}^i \dot{z}^k \dot{z}^l = \sum_k A_k^i \dot{z}^k, \quad (10)$$

where,

$$A_k^i = (\alpha_i + \beta_{ik}) \frac{\partial \ln(1 + \Omega)}{\partial z^k}. \quad (11)$$

The original equations (4) play the role of constraints to Eqs. (10).

Consider the basic geometric properties of the space $\mathcal{A}_{N-1}(\Gamma_{kl}^i)$.

The curvature tensor

$$R_{lki.}{}^q = \frac{\partial \Gamma_{li}^q}{\partial z^k} - \frac{\partial \Gamma_{ki}^q}{\partial z^l} + \sum_p \Gamma_{kp}^q \Gamma_{li}^p - \sum_p \Gamma_{lp}^q \Gamma_{ki}^p \quad (12)$$

can be written using (9) as follows:

$$R_{kql.}{}^j = (1 + \Omega)^{1/2} \left[\frac{\partial^2}{\partial z^k \partial z^l} (1 + \Omega)^{-1/2} \delta_q^j - \frac{\partial^2}{\partial z^q \partial z^l} (1 + \Omega)^{-1/2} \delta_k^j \right]. \quad (13)$$

The Ricci tensor, $R_{ql} = \sum_k R_{kql.}{}^k$, is

$$R_{ql} = (1 + \Omega)^{1/2} (2 - N) \frac{\partial^2 (1 + \Omega)^{-1/2}}{\partial z^q \partial z^l}. \quad (14)$$

Then, we can verify that

$$R_{kql.}{}^j = \frac{1}{2 - N} (R_{kl} \delta_q^j - R_{ql} \delta_k^j). \quad (15)$$

The case $N = 2$ apparently requires special consideration. If $N > 2$, the curvature tensor satisfies the criterion of the projectively Euclidean space [12, p.540]. Hence, we get

Theorem 2 *The space $\mathcal{A}_{N-1}(\Gamma_{kl}^i)$ supplied with the affine connection (9) is a projectively Euclidean space.*

The form of the affine connection Γ_{kl}^i (9) leads to the statement that $\mathcal{A}_{N-1}(\Gamma_{kl}^i)$ is an equiaffine space [13, §41]. In such a space, a volume exists which is invariant under the parallel transport of vectors. The volume element spanned on vectors $\xi_k^{i_k}$ has the form

$$V = \sum_{i_1, \dots, i_{N-1}} e_{i_1 \dots i_{N-1}} \xi_1^{i_1} \dots \xi_{N-1}^{i_{N-1}}$$

which conserves under parallel transport of ξ_k^{ik} . Here $e_{i_1 \dots i_{N-1}} = \sigma \epsilon_{i_1 \dots i_{N-1}}$, $\epsilon_{i_1 \dots i_{N-1}}$ is completely antisymmetric symbol, $\epsilon_{1 \dots N-1} = 1$. In the space $\mathcal{A}_{N-1}(\Gamma_{kl}^i)$, σ serves as a fundamental density and is defined by the following condition

$$\sum_s \Gamma_{ks}^s = \frac{\partial \ln \sigma}{\partial z^k}.$$

For Γ_{kl}^i of the form (9), we obtain: $\sum_s \Gamma_{ks}^s = \partial \ln(1 + \Omega)^{N/2} / \partial z^k$. Then, we have the theorem true.

Theorem 3 *The fundamental density of the space $\mathcal{A}_{N-1}(\Gamma_{kl}^i)$ with the connection (9) has the form $\sigma = (1 + \Omega)^{N/2}$.*

The considered geometry is of a special interest when the geodesical equations are exactly integrated. In this case the allele coupling in our approach is represented as a pure curving of the population variable space. It is connected with the following form of the fitness matrix $\omega_{\alpha\beta}$ in the Fisher system (2): $\omega_{ij} = \omega_{Nj}$, $j \neq N$; $\omega_{iN} \neq \omega_{jN}$, $i \neq j$. As a variant of a real genetic system resulting in such form of the matrix $\omega_{\alpha\beta}$ we can suggest a system with the chromosomal imprinting found in the course of the gametogenesis of mammals. According to [10], the result of the imprinting is that the same allele is included into a genome of a zygote in active or in non-active state. The allele activity depends on its affiliation to the DNA of male or female gamete. Molecular mechanism of the chromosomal imprinting is based on the differential methylation of DNA in the course of the gamete maturation.

For weak 'external field' A_k^i , that takes place under the condition

$$\alpha_i + \beta_{ik} = \varepsilon \gamma_{ik}, \quad \varepsilon \ll 1, \quad (16)$$

(α_i , β_{ik} are of the form (5)) the analysis of the motion can be carried out in two steps. First, we consider the motion along the geodesic lines, then we account for the 'external field' A_k^i perturbatively.

4 Integration of the geodesic equations

The system (10) has the form of equations of geodesics of the space $\mathcal{A}_{N-1}(\Gamma_{kl}^i)$ under the condition $A_k^i = 0$. Eqs. (10), with account of (9), can be written in the form:

$$\ddot{z}^j + \dot{z}^j \sum_l \frac{\partial \ln(1 + \Omega)}{\partial z^l} \dot{z}^l = 0, \quad (17)$$

or

$$\ddot{z}^j + \dot{z}^j \frac{d}{dt} \ln(1 + \Omega) = 0.$$

The first integration gives

$$\dot{z}^j = \frac{c_j}{1 + \Omega}, \quad (18)$$

where c_j — are integration constants.

Notice that the original equations (4) under the condition (16) take the form:

$$\dot{z}^j = \frac{\alpha_j}{1 + \Omega} + \frac{\varepsilon \sum_k \gamma_{jk} \exp(z^k)}{1 + \Omega}. \quad (19)$$

Putting $\varepsilon = 0$, we see that the restrictions being imposed by Eqs. (4) on the system (17), are reduced to

$$c_j = \alpha_j. \quad (20)$$

Let us now integrate Eqs. (18) under the condition (20). Without loss of generality, we can assume

$$z^j = \alpha_j \varphi(t) + b_j. \quad (21)$$

Here b_j are the integration constants, and the function $\varphi(t)$ is determined by the equation

$$\dot{\varphi}(t) = \frac{1}{1 + \Omega}, \quad \Omega = \sum_k \exp(\alpha_k \varphi(t) + b_k),$$

whose implicit solution is

$$\varphi(t) + \sum_k \alpha_k^{-1} \exp(\alpha_k \varphi(t) + b_k) = t - t_0. \quad (22)$$

Let us redefine the parameter in the equations of integral lines (21) setting $\tau = \varphi(t)$. Then the time t is explicitly expressed in terms of the parameter τ as

$$t - t_0 = \tau + \sum_k \alpha_k^{-1} \exp(\alpha_k \tau + b_k). \quad (23)$$

Eqs. (21) take the form of equations of the motion with the constant velocity α_j with respect to the 'new time' τ for an effective particle:

$$\dot{z}^j = \alpha_j \tau + b_j. \quad (24)$$

For a weak 'external field' A_k^j (16), Eqs. (10) can be solved approximately as follows.

Let us put

$$z^j = \alpha_j \tau + b_j(\tau) \quad (25)$$

and take b_j to be a slowly varying function of τ . Substituting (25) into (19) and taking into account (20), we get:

$$\frac{db_j}{d\tau} = \varepsilon \sum_k \gamma_{js} \exp(\alpha_s \tau + b_s). \quad (26)$$

In the first approximation (putting b_s to be constants in the right-hand side of (26)) we obtain:

$$z^j = \alpha_j \tau + \varepsilon \sum_k \gamma_{jk} \alpha_k^{-1} \exp(\alpha_k + b_k(0)), \quad (27)$$

where $b_k(0)$ are the constants of integration.

5 Conclusion

Discuss a biological sence of the parameters α_i , β_{ij} in (4). If $\beta_{ij} = 0$ then the system (4) is reduced to the dynamics of haploid populations. A detail analysis of such systems was performed in [9]. The parameters α_i in this case have a meaning of specific rates of reproduction of separate genotypes (the Maltusian parameters in ecological terms). Thus, it is the matrix β_{ij} (not the complete matrix $\omega_{\alpha\beta}$) which is effectively responsible for the alleles coupling. It is not evident from the original Fisher system (2). The allele coupling is represented as a curvature in the geometry of the population variable space. The tensor (12) is the measure of this curvature and it is completely determined by the value $\ln(1 + \Omega)$. Note that this value is expressed in the population variables in the following form: $\ln(1 + \Omega) = \ln(1/p_N)$. In its turn, $\ln(1/p_N)$ is a measure of an information of the N -th allele in the population by Shannon. It is clear, the more rarely the N -th allele occurs in the population the larger is the curvature of the space associated with the selection dynamics. Let us also emphasize that the basic geometrical characteristic of this space is completely determined by encounter frequency of N -th allele. Among all the possible variants of the matrices $\omega_{\alpha\beta}$, a particular interest has the case $\varepsilon = 0$ in (16) when the system (4) is integrated explicitly and its solution is reduced to the uniform rectilinear motion (24) by the redefinition of time variable. This case is similar to the Eigen selection dynamics in haploid populations and, as it is shown in [9], admits the Hamiltonian form of the dynamic equations. Let us note that in this case the allele coupling is effectively reduces to time flow change according to (23).

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